THE CASE AGAINST THE TRANSFER OF *DRYANDRA* TO *BANKSIA* (PROTEACEAE)[1]

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ABSTRACT

The transfer of *Dryandra* R. Br. to *Banksia* L. f. was based on the use of holophyly (monophyly s. str.) as an essential criterion for recognition of taxa. The transfer was significant in scope and focuses on two iconic genera of plants in Western Australia. It has been accepted by some and rejected by others. It is one of many examples in a debate that pits recent genetic analysis against centuries of field and herbarium studies, and cladists against classical taxonomists. I argue that: (1) there are sound morphological characters distinguishing *Dryandra* from *Banksia* and they should be maintained as genera; (2) paraphyly should be accepted in biological classification; (3) scientifically, and for a morphologically complex genus of 137 specific and infraspecific taxa, the use of 11 taxa for the molecular analysis of *Dryandra* was insufficient; (4) some morphological data, mapped onto the cladogram a posteriori, were incorrect; (5) molecular cladistic approaches should complement rather than override pre-existing and extensive classifications based on phenotypic traits; (6) the acceptance of the transfer for the Australian Plant Census was premature according to guidelines published by Australian herbaria.

Key words: Australian Plant Census, *Banksia*, cladistics, *Dryandra*, molecular analyses, paraphyly, Proteaceae.

Over the last four decades, cladistics has become a widely used tool in plant systematics, while molecular analyses have been used increasingly since the early 1990s. Genetic data have become a particularly powerful tool that has enlivened the field of systematics, especially in phylogenetic analyses. However, attempts to reconcile cladistic and traditional classifications have often been controversial (Hörandl & Stuessy, 2010). The purpose of this paper is to review and critique the application of molecular phylogenetic approaches to the systematics of two Australian genera of Proteaceae, *Banksia* L. f. and *Dryandra* R. Br. The intent is to demonstrate that the transfer of *Dryandra* to *Banksia*, which was based on strict adherence to the debatable cladistic concept of holophyly (monophyly s. str.), was not well grounded scientifically, has led to a loss of information, caused confusion among the users of plant names, and joins similarly based transfers of genera in other families. Examples of problems caused by over-reliance on cladistic approaches in plants and animals, especially involving molecular phylogenetic analyses, are used to pinpoint the issues involved in reclassifying life forms based on holophyly. In this case, and in others discussed here, while the data are claimed to show that *Dryandra* makes *Banksia* paraphyletic, the evidence presented for the holophyly of the two genera when combined is based on insufficient sampling.

Stuessy (2009a) and Hörandl and Stuessy (2010), among others, have discussed the different concepts of monophyletic—the original meaning of Haeckel (1866) to define simply a group with a common ancestor, contrasting with the narrow cladistic concept of Hennig (1966) to define a group that includes all the descendants of a common ancestor. The latter has been given another term, "holophyletic," first suggested by Ashlock (1971). The term is used in this paper except in quotes where monophyly is retained rather than assume the meaning intended by the author(s).

In 2007, Mast and Thiele published a paper combining *Dryandra* with *Banksia*, with a further paper later that year covering names that were overlooked in the first paper (Thiele & Mast, 2007). The transfer was based on phylogenetic analyses of molecular (genetic) data. The Australian herbaria quickly adopted the change for the Australian Plant Census, but both the transfer and its rapid acceptance were met with resistance from many users of plant names. Was such a wholesale change justified and necessary? The merger certainly ran counter to conclusions reached in my research of over 50 years in the field, in the herbarium, in horticulture, and in the literature (e.g., George, 1981, 1984, 1996, 1999a, 1999b; Collins et al., 2008). Morphologically, the two genera are readily distinguished and recognizable, although I have deliberated whether certain small groups within each genus should be recognized at

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generic rank, in particular *Banksia* subg. *Isostylis* and *Dryandra* subg. *Hemiclidia* and *Dryandra* subg. *Diplophragma*. Disagreement and dismay at the merger from many sources in the community prompted Thiele to publish several popular articles seeking to explain this change to a wider audience (e.g., Thiele, 2008a, 2008b, 2008c).

When Nomenclature Is Changed

The International Code of Nomenclature for algae, fungi, and plants (ICN; McNeill et al., 2012) and its provisions are clear—nobody is obliged to follow a change simply because it is the latest published or because certain institutions have adopted it (George, 2008; see also below). Under the ICN, taxonomic names of plants are available for use if they meet certain criteria, and, if a plant has more than one available name, no further direction is given on how to choose which binomial to use. In the case at hand, the names of all except one species of *Dryandra* meet the criteria, and users can choose whichever generic name they prefer. The exception is a taxon named as *Banksia recurvistylis* K. R. Thiele (Thiele, 2009), for which I present a new combination as a subspecies in *Dryandra* elsewhere (George, 2012). Likewise, there is no mandatory requirement to follow the Australian Plant Census, coordinated by the major Australian herbaria.

The Australian Native Plants Society (formerly Association of Societies for Growing Australian Plants), with several thousand members, has a number of study groups for those interested in particular genera or groups. Among these are the Dryandra Study Group and the Banksia Study Group. The merger of the two genera has been debated in their newsletters (e.g., Cavanagh, 2008a, 2008b; Barrow, 2009) and they continue to accept both genera in the traditional sense. Under the ICN, this is perfectly acceptable, but we have the awkward situation of the "custodians" of plant nomenclature in Australia—some major herbaria—taking one stand, and the users another (including the Catalogue of Plants, Botanic Gardens of Adelaide, 2010). It is apparent that this dichotomy cannot continue indefinitely.

Dryandra and *Banksia*

Dryandra and *Banksia* comprise subtribe Banksiinae of tribe Banksiae, subfamily Grevilleoideae, Proteaceae. Currently, *Banksia* s. str. contains 78 species (with 20 infraspecific taxa) placed in two subgenera, one with 75 species in three sections and 13 series, the other with just three species (George, 1999a; Collins et al., 2008). Most (61) species are endemic in southwestern Australia; 16 species occur in moister areas of eastern and southeastern Australia; and one species occurs across tropical Australia and in New Guinea. *Dryandra* contains 94 species (with 43 infraspecific taxa) in three subgenera (George, 1999b; Cavanagh & Pieroni, 2006). As in *Banksia*, one subgenus contains the majority of the species, 91 placed in 24 series, the other subgenera having two and one species. *Dryandra* is endemic in southwestern Australia.

Two apomorphic states are clear cut in distinguishing *Dryandra* from *Banksia*. First, the receptacle in *Dryandra* is flat or only slightly convex or concave; in *Banksia* it is ovoid to cylindrical. Second, the common and floral bracts (not to be confused with the involucral bracts subtending the whole inflorescence) in *Dryandra* are openly arranged; in *Banksia* they are tightly packed—this distinction is easy to see but it has not been quantified. Thiele and Ladiges (1996: 665) referred to it, as did George (1999b). It has not been mentioned in any of the papers supporting the transfer of *Dryandra* to *Banksia*. Further characters are useful but are not wholly inclusive in distinguishing *Dryandra*: conspicuous, persistent involucral bracts; common and floral bracts that enlarge as the fruit develops; thinner follicles, in many species easily detached. Figure 1 shows the type species of each genus.

In his popular presentations, Thiele has used two diagrammatic "trees" to explain the transfer (Thiele, 2008b, 2008c). One (his fig. 1 in both papers) shows *Banksia* and *Dryandra* arising (evolving) from the same point and is said by him to be the traditional view. The other (his fig. 2) shows *Dryandra* arising from within *Banksia* and is said to be a new result, giving a new understanding, that justifies having to place *Dryandra* in *Banksia*. In fact, the latter "tree" is the traditional view of the relationship of *Dryandra* and *Banksia*. It confirms the view that systematic botanists have held since Robert Brown published the name of the genus *Dryandra* in 1810—to place the genus at the pinnacle of an assumed developmental or evolutionary line within Australian Proteaceae with the implication that, in modern terms, it probably arose out of *Banksia* and is the most highly evolved genus. In other words, contrary to Thiele's claim, the "new" tree confirms the traditional view.

Aspects of the Molecular Work on *Dryandra* and *Banksia*

Data on the material sampled for the molecular analyses are given for Mast and Givnish (2002) on the website of the *American Journal of Botany* at <http://ajbsupp.botany.org/v89/mast.doc> (accessed 2 April



Figure 1. A, B. *Dryandra formosa* R. Br., the type species of *Dryandra*. —A. Headlike inflorescence (photograph: A. George). —B. Infructescence showing involucral bracts and follicles just beginning to open (photograph: A. Cavanagh). C, D. *Banksia serrata* L. f., the type species of *Banksia*. —C. Spikelike inflorescence (photograph: A. George). —D. Infructescence showing two upper follicles still closed, the others opened, and persistent old, unfertilized flowers (photograph: M. Pieroni).

2010). There we find that cultivated material with no vouchers cited was used for four taxa (*Banksia ornata*, *B. penicillata*, *B. saxicola*, *B. spinulosa* var. *neoanglica*), and no source or voucher is cited for a further six taxa (*B. gardneri* [variety not stated], *B. laevigata* subsp. *fuscolutea*, *B. conferta*, *B. paludosa* [variety not stated], *B. ericifolia* "var." [correctly subsp.] *macrantha*, *B. meisneri* "var." [correctly subsp.] *meisneri*), so the determination of these taxa cannot be verified and no repeat of the sampling can be made. They can be reanalyzed only with new samples that may not be identical genetically. The later papers are based on the same samples with several cited additions (Mast et al., 2005: 79). Interestingly, Mast and Thiele (2007) mentioned *Dryandra subulata* as an exception to the holophyly of *Dryandra* because it fell "within a clade of *Banksia* in the cpDNA phylogeny," but the species is not shown in any of the analyses and no voucher is cited.

In transferring *Dryandra* to *Banksia*, Mast and Thiele (2007) stated that "molecular and morphological characters provide evidence that *Banksia* is

paraphyletic with respect to *Dryandra*" and referred to three earlier papers. In the first paper, Mast (1998) sampled the entire internal transcribed spacer region of the nuclear ribosomal DNA (ITS) from 18 taxa of *Banksia* and five of *Dryandra*. He also sampled the *trnL/trnF* region from two non-coding chloroplast DNA (cpDNA) regions from 10 taxa of *Banksia* and four taxa of *Dryandra* (in all papers the two genera in subtribe Musgraveinae were also sampled). In the second paper, Mast and Givnish (2002: 1312) expanded the circumscription of the cpDNA to "chloroplast *trnL* intron, *trnL 3′* exon, and *trnL/trnF* spacer." They sampled 84 taxa of *Banksia* and five taxa of *Dryandra* . . . "for each of these taxa, two to five cpDNA regions were sampled depending on each taxon's function in four sampling strategies" (p. 1312). The regions were *trnL* intron, *trnL/trnF* spacer, *trnT/trnL* spacer, *rp116* intron, and *psbA/trnH* spacer. For the third survey, Mast et al. (2005) sampled 29 taxa of *Banksia* and eight taxa of *Dryandra* and added data from two coding regions, the *matK* and *atpB* chloroplast genes, and the nuclear *waxy* gene. They used the same collections as in the previous research, with the addition of three new collections of *Dryandra* (cited in the paper). Descriptions of the DNA sequence alignments were summarized in Table 2 of Mast et al. (2005: 82).

The sampling of *Banksia* appears adequate (i.e., 84 of 98 taxa). In contrast, only a small proportion of *Dryandra* taxa was sampled. Three taxa of *Dryandra* sampled in the first paper were not used again, and all those in the second were also used in the third. Hence the total number from this genus sampled was 11. Mast et al. (2005: 85–86) considered it an adequate number for their deliberations on the generic status because it represented the three subgenera of the genus, but it is an inadequate number on which to base far-reaching decisions on where to place individual taxa within a generic schema (i.e., transferring taxa to another genus without studying them). As shown by the large number of series, *Dryandra* is highly complex morphologically, so, until a more comprehensive survey is done, we do not know if or how this uneven representation affected the results. Mast and Thiele (2007: 63) referred to "wider sampling of all subgenera and series [of *Dryandra*] except the monotypic series *Decurrentes*" but chose to exclude the data from their paper.

Further questions arise. In Mast and Givnish (2002), all the species analyzed to that time were included in figures 3 and 6 and there are 12 unresolved groups. In Mast et al. (2005), why do none of the trees show all the species of *Banksia* that were analyzed for this and earlier papers? How were the species included in the trees chosen? Did the omitted species show different or anomalous results?

The question of sample size is of great importance, and there is no doubt that the DNA chosen for these analyses represents a small fraction of the total. As Stuessy (2009a: 278) has written, regarding ITS sequences, "If only one sample per taxon is analyzed, the results can be misleading [the same may be said for any character or state used in a systematic study]. The best defense is to sequence three or more accessions per taxon to look for possible multiple copies of the gene." In their early work on *Banksia* and *Dryandra*, Mast and Givnish (2002) "did not sample ITS data at their finer taxonomic sampling because divergent ITS paralogues were discovered among the perhaps thousands of copies of this region . . . and the paralogues from each individual were not always resolved as monophyletic in the phylogenies" (Mast et al., 2005: 79). Mast et al. (2005) therefore extended their sampling to include the waxy gene. Nonetheless, the analyses were presumably based on single samples of each taxon, from the citation of the taxa studied and the vouchers listed (Mast & Givnish, 2002). Despite their uncompromising reliance on holophyly, Edwards et al. (2010, figs. 2 [e.g., AT(1), AT(3)] and 4 [e.g., MH325, GBfoli]) used several samples determined as the same species in their analyses and in several instances these came out separately within the complex, e.g., *Melaleuca leucadendra* (one sample on a separate subclade from the other two), *M. quinquenervia*, and *M. argentea* (their fig. 2).

Would the results have been the same if the whole genome were analyzed rather than several gene regions? Thiele himself (2008a: 14, footnote) also posed the question "how can we possibly get any meaningful answer from such a tiny sample?" His answer (loc. cit., in the text) was that Mast's analyses of several genetic regions "pointed to the same answer (at least in broad outline)" as his own (Thiele's) analyses of morphological and anatomical characters in *Banksia* (no such analysis for *Dryandra* has yet been published). This is standard practice, when several genetic markers are used to carry out maximum likelihood and maximum parsimony analyses (Krane & Raymer, 2003). Mast and Givnish (2002: 1315) reported that "when the relationships within subtribe Banksiinae are compared on strict consensus trees derived from different strategies, there is no topological conflict." There is conflict, or at least different levels of resolution, in the three trees given in Mast et al. (2005; fig. 3A, B), e.g., in the position of *B. elderiana*, *B. media*, and *B. coccinea*,

and in the relationship of a group including *B. elderiana*, especially between figures 3A and 4. In the ITS analysis there was no resolution at all within */Phanerostomata*. Mast et al. (2005) noted the discrepancy in the branching in their cpDNA and ITS analyses but concentrated on the 100% support for the holophyly of the subtribe Banksiinae. Again, would samples of further species, and more samples per species (especially widely distributed, variable ones such as *D. sessilis* and *B. marginata*), have resolved any of this conflict and given more confidence in the results? Later, they stated that "exploration of incongruence among the datasets is outside of [sic] the objectives of this paper" (p. 85), even though the third of their objectives was to "discuss how this [DNA sequence evidence] might influence the biological community's treatment of the two genera in the future" (p. 79). I acknowledge that the authors' focus was on the larger picture of overall groupings and how these should be interpreted at the generic level, but I suggest that results showing poor resolution between the various genetic regions should have been investigated further, especially since these are such important genera. Surely, it is not sound taxonomic practice to make nomenclatural changes without studying every species involved.

Interestingly, He et al. (2011) obtained the sequences of Mast and Givnish for five chloroplast DNA regions from GenBank and reanalyzed them to produce a molecular phylogeny. The programs used were not mentioned. The resultant tree shows general agreement with those of Mast et al. but "with better resolution of more recent divergences" (He et al., 2011: 187). The divergence into */Cryptostomata* and */Phanerostomata* remains, as does the grouping of *Dryandra* as a monophyletic group arising out of */Cryptostomata*. There are, however, marked differences in the position of species such as *Banksia attenuata*, *B. tricuspis*, *B. oblongifolia*, and *B. quercifolia*. */Phanerostomata* appears as the same heterogeneous group of taxa. This also suggests that further research and analysis are needed to investigate the relationship of these taxa.

Paraphyly and Holophyly in Classification

Strict proponents of cladistic classification accept only holophyletic taxa and reject paraphyletic taxa, despite a growing number of papers arguing that this is illogical, ignores many morphological characters, and cannot be applied comfortably to a phylogeny. Taken to an extreme, logical conclusion, all flowering plants would be placed in a single genus, or even species (e.g., Brummitt, 2006: 268). While no one would formally propose this, it becomes relevant at smaller scales. For example, Humphreys and Linder (2009: 1066) wrote that "strict adherence to this statement [recognizing larger monophyletic groups] would mean equating the entire subfamily [danthonioid grasses] with . . . *Danthonia* DC. As this would have several practical disadvantages today, including vast nomenclatural disruption, we do not follow this route." In other words, cladistic classification can be incompatible with what we see around us and impractical for a binomial classificatory system. A number of experienced systematists have presented these arguments, and, to my knowledge, no cladist has answered these criticisms satisfactorily (Schmidt-Lebuhn [2012], however, has made a biased attempt in this direction)—for succinct assessments, see, e.g., Brummitt (2006, 2008), Hörandl (2007, 2010), Stuessy (2009b), and Hörandl and Stuessy (2010). Nelson et al. (2003: 296) responded to Brummitt's (2002) challenge to "draw a phylogenetic tree . . . divided fully into Linnaean taxa without being paraphyletic." However, they drew generic rank across their tree at the third level of nodes from the apex to give four similar taxa (genera). This was one node level above the divergence where major character change occurred in Brummitt's tree that led to one very distinctive genus and three branches representing morphologically similar taxa placed in a single genus. That is, they did not allow for a new taxon evolving very differently while the others remained similar, so that the first was recognized as a distinct genus that would be paraphyletic. This was pointed out by Brummitt (2003), and as far as I know, Nelson et al. (2003) have not responded in the literature.

Pfeil and Crisp (2005) also attempted to answer Brummitt's (2002) challenge to counter the charge that accepting only monophyletic (holophyletic) taxa is illogical. They undermined their argument, however, when, in discussing how to "chop up" a tree and referring to Brummitt's (2002: 32) figure 1, modified by the authors as their figure 2, they accepted the cladistic tenet that "taxa are defined by their shared ancestry rather than their conspicuous characters, that is, they should be monophyletic" (p. 52). They also assumed that Brummitt's (2002) suggested genera were "based on artificial groupings of species." They did not explain "artificial," but it appears that they meant paraphyletic groups even if these are distinguished by good morphological characters. Such characters are determined after sound study of the organisms, not arbitrarily as Pfeil and Crisp (2005) claim. Brummitt gave several examples of taxa in which there are good characters

defining morphologically cohesive ("natural") groups that molecular analysis showed to nest one in another, e.g., Cactaceae within Portulacaceae (and not just within Portulacaceae but within one genus thereof, *Talinum*).

The statement by Pfeil and Crisp (2005: 52) that Brummitt (2002) has created the conflict between paraphyletic and monophyletic (holophyletic) classifications is incorrect. Brummitt was describing a conflict that has arisen over some years from the different approaches between taxonomists who take all characters into account and those who rigidly follow the cladistic tenet of holophyly, and disregard characters that are seen as plesiomorphic. Hörandl and Stuessy (2010: 1641–1642) also discussed the controversy and conflict that have arisen from the refusal by many workers to accept paraphyletic groups, writing: "When cladists elected to allow only holophyletic groups in classification, this excluded paraphyletic groups that were accepted by evolutionary workers. This led to conflict with traditional classifications that had frequently accepted paraphyletic taxa because of shared similarity." Another error by Pfeil and Crisp was their attribution (p. 53) of the following statement to Brummitt: "Hennig fatally ignored Darwin's observation ... that evolutionary classification depends on two factors, descent and modification. Hennig ignored modification and thought classification could be based only [word omitted by Pfeil and Crisp] on phylogeny irrespective of characters." In writing this, Brummitt attributed it to Ernst Mayr. Pfeil and Crisp chose not to comment on Brummitt's subsequent statement, that Hennig attempted "to equate the hierarchy of descent directly with the hierarchy of Linnaean classification, but, as I hope I have demonstrated, these are incompatible" (Brummitt, 2002: 35).

Pfeil and Crisp's (2005: 53) conclusion that "the solution to Brummitt's conundrum is to use phylogenetic trees to define higher taxa—not an arbitrary subset of the characters that produced the trees" is no solution at all. It simply confirms their strict adherence to holophyly. They did not address Brummitt's challenge to "draw a phylogenetic tree and divide it into families and genera without creating paraphyletic families and genera" (Brummitt, 2002: 33).

As Brummitt (2006: 269) has written, sinking morphologically distinct taxa into a paraphyletic parental taxon merges them into an "amorphous plesiomorphic soup" and is a denial of evolution—it does not recognize newly evolved taxa. "Since, in the cladist view, no family or genus can have evolved from another one, it is effectively a denial of evolution having taken place. ... To overcome these objections to cladistic taxonomy, its proponents argue that we are dealing only with present-day taxa and must ignore ancestors because we do not have them and so cannot name them. So at the same time as they define paraphyly in terms of ancestry, they insist on ignoring ancestry. This is not logical."

To put it another way: just because a group of taxa is nested in a molecular or cladistic analysis within others is no logical reason to lump them taxonomically. It's a matter of where you draw the line or lines delimiting rank on a tree. In the case of *Banksia* and *Dryandra*, instead of lumping the operational taxonomic units (OTUs) into a single taxon, this could have led to recognition of more taxa and still been concordant with the data. Mast and Thiele did not explain why they did not wish to recognize tribe Banksiinae at generic rank and include *Musgravea* and *Austromuellera*. Two analyses of Mast et al. (2005) show 100% and 92% bootstrap support for their inclusion with *Banksia* and *Dryandra* in a single taxon, and retaining them as separate genera makes them paraphyletic with respect to *Banksia*. Perhaps this is an instance of Pfeil and Crisp's (2005: 52) "but it's so different" (BISD) argument? If more genera were included in any cladistic analysis, those higher on the cladogram might (or almost certainly would) make those lower down paraphyletic, necessitating lumping more genera in order to maintain holophyly. An example of including more genera is a paper by Edwards et al. (2010), in which all nine genera of the tribe Melaleuceae (Myrtaceae) were analyzed and *Melaleuca* found to be paraphyletic, leading them to conclude that all nine must be combined as a single genus. The taxonomic sample was small, 50 species of a total of ca. 335 for the tribe, with 36 species of *Melaleuca* (current total 259) sampled, one of *Calothamnus* (41), three of *Beaufortia* (15), two of *Eremaea* (15), one of *Regelia* (6), two of *Conothamnus* (3), one of *Phymatocarpus* (3), two of *Lamarchea* (2), and one of *Petraeomyrtus* (1). While bootstrap support for the tribe was strong, that for the three clades within it was less so—56%, 81%, and 67% (their fig. 1). Within their clade A (their fig. 2), which contains the genera currently recognized to be distinct from *Melaleuca*, support for some nodes was weak, with a bootstrap value of 51% for the node from which all genera except *Lamarchea* and *Beaufortia* diverge from *Melaleuca*, and support for *Beaufortia* was only 54%. Several species of *Melaleuca* came out in the "other genera" clade. The authors proposed merging all genera in *Melaleuca* because, firstly, "the morphological

characters examined in this study were found to have high levels of homoplasy and to lack diagnostic ability" (Edwards et al., 2010: 753). They did not elaborate on how they came to these conclusions, nor did they say whether they had looked for more than the 27 characters listed in their Appendix 1. Secondly, they considered that "it is desirable to avoid generation of many new genera with few representatives." There is no scientific basis for this view. The proposal to merge these genera appears to be unsound.[1]

A telling comment comes from Cavalier-Smith (2010: 111) who wrote: "Hennigian cladistics emphasizes only lineage splitting, ignoring most other major phylogenetic processes. Though methodologically useful it has been conceptually confusing and harmed taxonomy, especially in mistakenly opposing ancestral (paraphyletic) taxa."

Comments by Grant (2003: 1268) are pertinent:

> Cladistics is based on inferred phylogenies, which makes for an uncertain foundation. Phylogenies of groups above the species level are, with rare exceptions, unverifiable hypotheses. Taxonomic systems are based on observable characters and do not rest on phylogenetic hypotheses, although taxonomists may (and do) weight characters and states differently.
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> . . . the information base . . . is very broad in taxonomy in which no class of characters is excluded from consideration. It is narrower in morphological cladistics because of the exclusion of certain types of potentially valuable characters, and it is extremely narrow in molecular cladistics. Taxonomy has a more inclusive empirical foundation than cladistics.

Stuessy (2009b: 72) has pointed out that cladistics has put interpretation of characters back into biological classification but at a cost: it focuses solely on branching patterns and reduces the information content. More recently, Stuessy and Hörandl (2010: 1642) have written:

> Hennigian and post-Hennigian cladistics have disregarded evolutionary data for the main purpose of constructing the branching pattern. The data of importance become the synapomorphies, whereas autapomorphies are discarded as noninformative. Emphasis on holophyly in a quantitative method of phylogeny reconstruction has resulted in a narrower (and less informative) approach to biological classification. Cladistic principles stress a restrictive hypothesis, that of dichotomous splitting of a lineage into two new lineages, resulting in extinction of the ancestor. Whether other evolutionary processes (e.g., budding and merging) are involved is neither tested, nor verified, nor falsified, but rather neglected a priori (Hörandl, 2010). Statistical tests of tree topologies, e.g., bootstrapping, support tree topologies under the assumption of dichotomies, but they do not test the assumptions themselves. Cladograms are useful tools to formulate specific hypotheses, but because of their theoretical restriction, they are not sufficient to yield robust evolutionary conclusions.

Pfeil and Crisp's assertion (2005: 53) that "the most recent common ancestor of e.g., a pair of genera, should not logically belong in either descendent genus" (repeated a little later as "the ancestral organism cannot have been a member of either modern genus") is itself not logical. The parent of an offspring that leads to a new taxon may survive for a long time and remains within its original taxon—it doesn't change its position in a classification because it has produced offspring. The line of descent of the original ancestor may continue through one descendant while a new line evolves through another (Hörandl & Stuessy, 2010: 1645).

Pfeil and Crisp (2005: 52) argued that paraphyly "perpetuates a classification that obscures information and reduces predictive power." In the case of *Dryandra* and *Banksia*, the reduction of *Dryandra* to a single series within *Banksia* in order to make the latter holophyletic has created a classification that causes just this loss.

Stace (2005: 1000) also had reservations about monophyly (holophyly), writing: "I personally advocate recognising paraphyletic taxa if this produces the most predictive classification, and in my view an absolute insistence on monophyly whatever the circumstances amounts simply to dogma. A monophyletic system of classification that is not the most predictive available becomes a special purpose classification. I would say that a phylogenetic special-purpose classification is about as practically useful as the party bore who details his troubled journey there to anyone who will listen."

The importance of accepting paraphyletic groups is summarized by Hörandl and Stuessy (2010: 1650):

> Above the species level, retention of paraphyly and holophyly is essential for the theoretical foundation of taxa through natural processes (common ancestry) and hence for predictivity. Information content and practicability, however, are needed as additional criteria to translate natural taxa into a formal classification. Information content and practicability are dependent on human perception, human logic, terminology, and utility of ordering systems of organisms. These anthropocentric aspects are obviously important for classification, as a global information system for organisms must be provided for the scientific community and for society in general. These principles are violated if classifications abandon paraphyletic taxa that are actually monophyletic s.l., although they may not appear as holophyletic clades in

[1] Despite these reservations (in particular the small taxonomic sample), and with no further research, the merger of all genera into *Melaleuca* has now been published (Craven et al., 2014). It is to be hoped that the Australian herbaria will follow their guidelines when assessing this for the Australian Plant Census. [Note added in proof.]

cladograms. Because of shared ancestry, paraphyletic taxa often have high phenotypic similarity and information content.

It is unfortunate that Mast and Thiele and their coworkers have not addressed the problem of paraphyly in their work on *Banksia* and *Dryandra*. Indeed, Mast et al. (2005: 86) wrote that "It is not within the scope of this paper to critically evaluate the place of paraphyletic taxa in taxonomy ...." Given that two major, well-known Australian genera are involved, and that paraphyly is a critical issue (as indicated by inclusion of the term in the title of their paper), it should have been discussed.

Mast and Thiele (2007: 63) united *Dryandra* with *Banksia* because their analyses "showed strong evidence for the paraphyly of *Banksia* with respect to *Dryandra*." They stated that "published and molecular evidence provide strong support for the monophyly [holophyly] of *Dryandra*," but this was based on limited sampling of the taxon. While they had strong support for the group containing both *Dryandra* and *Banksia*, they cannot show that a combined *Dryandra* and *Banksia* is monophyletic (holophyletic) until *Dryandra* is sampled much more extensively.

I support the recognition of paraphyletic taxa in Linnaean classification, and maintain that, given present data, *Dryandra* is an easily recognized, holophyletic taxon that should be accepted at generic rank. *Banksia* s. str., considered paraphyletic by Mast and Thiele, should continue to be accepted pending further work. Whether *Dryandra* is, in fact, holophyletic remains to be shown by wider sampling. This may confirm that it is holophyletic, or show that both it and *Banksia* are polyphyletic. Given the morphological diversity of both genera, it is more likely that holophyly will be maintained only by recognizing more genera. Clearly, further research is needed to resolve the classification of these taxa.

Other Aspects

Thiele (2008b) wrote that, because some species of *Banksia* are related more closely to *Dryandra* than to other banksias, keeping the genera separate is a "serious anomaly." This need not be the case—it's obvious that, when a new organism evolves from a member of a large group, it is going to be related more closely to that member than to the others. At some point it (and its descendants) may then become different enough to be recognized as a new genus. It would have been valuable for Mast and Thiele to take their research further to investigate how best to resolve the three branches on their tree (Mast & Thiele, 2007: 64; see Fig. 1 below) leading to unlabeled parts of */Cryptostomata*. This may indicate which species or group of species is sister to *Dryandra* and show where research should be focused regarding the origin of the latter.

Thiele (2008c: 7) also claimed that their molecular analysis explains the distribution of *Dryandra* in southwestern Australia—it evolved from "its banksia ancestor ... after the south-west was isolated by increasing aridity, and none of its ancestors managed to cross the deserts." In fact, the analysis simply confirms what has been said many times—that many groups of plants and animals have evolved in southwestern Australia since the Nullarbor Plain and deserts formed (e.g., Hopper & Gioia, 2004). The analysis of He et al. (2011) also confirms that *Dryandra* arose after the formation of the Nullarbor Plain. This is an example of loss of information from combining *Dryandra* with *Banksia*: Barker et al. (2007) put the origin of a combined genus at 65 Ma (thus giving no indication for *Dryandra*), and Sauquet et al. (2009) determined it as ca. 50 Ma, whereas He et al. (2011), analyzing the genera separately, confirmed *Banksia* s. str. at the same age but placed the origin of *Dryandra* at ca. 15 Ma.

As support for a major generic change, the phylogeny shown in figure 1 of Mast and Thiele (2007: 64) is remarkably simplistic and misleading. It is said to be "modified from fig. 1b of Mast et al. 2005," but that figure is a photograph of *Dryandra ferruginea* and presumably the reference is to figure 2B (Fig. 2 in this paper). Compared with that figure, Mast and Thiele's figure 1 of 2007 has sprouted a third branch above "beaked follicles," explained with the statement in the caption that "the number [of lineages] is variable in the phylogenies inferred with each of the datasets" (p. 64). In order to find which taxa each branch of these figures leads to, one must try to reconcile them with figures 3 and 4 of Mast et al. (2005) but, because of a different style of branching, that is a difficult task.

On Morphology

Mast and Thiele's claim (2007: 63) that "morphological characters provide evidence that *Banksia* is paraphyletic with respect to *Dryandra*" was overstated, because they did not make a detailed morphological analysis of all taxa of *Dryandra*. Rather, a posteriori they placed a few characters on their molecular trees—see figure 2B of Mast et al. (2005) (Fig. 2 in this paper), given in simplified form as figure 1 in Mast and Thiele (2007). As argued by Assis and Rieppel (2011: 97), synapomorphy and monophyly are not the same thing and mapping

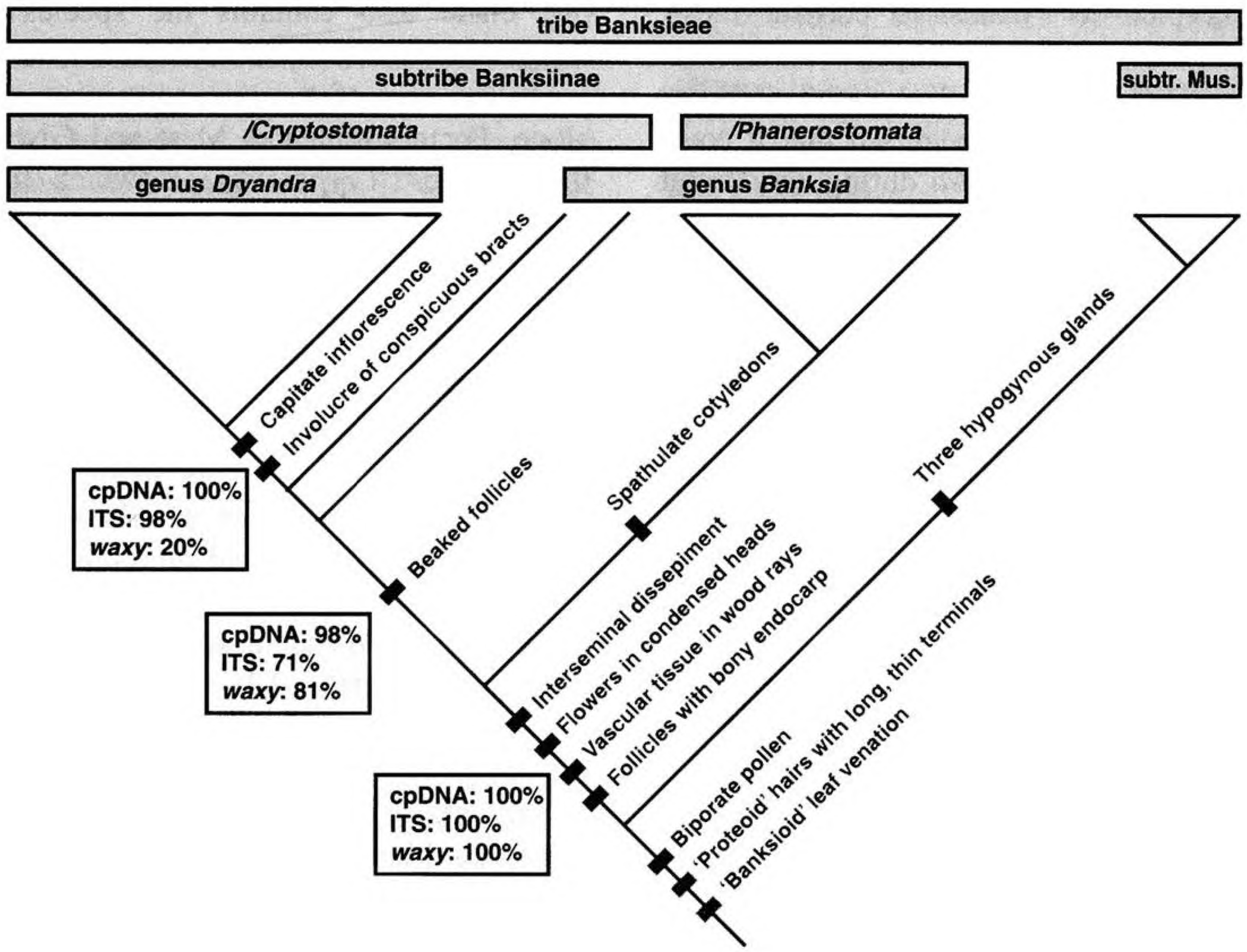


Figure 2. Figure 2B from Mast et al. (2005). Reproduced with permission from *Australian Systematic Botany* 18: 75–88 <http://dx.doi.org/10.1071/SB04015> (Mast et al.) Copyright CSIRO 2005. Published by CSIRO PUBLISHING, Collingwood, Victoria, Australia. Original caption: "Phylogenies reconstructed for members of the tribe [Banksieae] by Mast (1998) and this study using the two internal transcribed spacers of the nuclear ribosomal DNA (ITS), Mast and Givnish (2002) and this study using chloroplast DNA (cpDNA), and this study using the nuclear waxy gene resolve a paraphyletic *Banksia* with respect to *Dryandra*. Bootstrap frequencies for three branches as determined in this study are given in boxes adjacent to the branches. Mast and Givnish (2002) recognised a morphological synapomorphy for each of the clades formed at the basal split of the subtribe in the DNA phylogenies and referred to these as */Cryptostomata* and */Phanerostomata*. Note that 'Subtr. Mus.' is subtribe Musgraveinae, containing two monotypic genera."

This figure was reproduced as figure 1 in Mast and Thiele (2007), but with the lowest branch (leading to subtribe Musgraveinae) deleted, "subtribe Banksiinae" replaced by *Banksia*, the generic names *Dryandra* and *Banksia* deleted, and the names "subgen. *Banksia*" and "subgen. *Spathulata*" added to */Cryptostomata* and */Phanerostomata*, respectively. Also, a third, unresolved branch was added above the character "Beaked follicles" leading to */Cryptostomata*, with a note in the caption that the number of lineages is "variable in the phylogenies inferred with each of the datasets."

morphological characters onto a phylogenetic tree derived from molecular data is an empty procedure, since those characters have not been tested for congruence with the data from which the tree has been built. Further, a useful definition of a synapomorphy is "a shared, derived character state." Far from being character states, those applied here are, rather, complex character suites and, given the relatively large number of species being dealt with, possibly homoplasious, but further research would be needed to confirm or refute this. This aside, there are problems with these "synapomorphies." Below the first branch is shown "Flowers in condensed heads" and then, below the terminal branch leading to *Dryandra*, "Capitate inflorescence." Both phrases mean much the same thing. The lower one should be, say, "Flowers in condensed inflorescences/conflorescences on a woody receptacle." The upper is then correct. On the first branch, leading to */Phanerostomata*, "Spathulate cotyledons" is given as a synapomorphy, but as discussed below in regard to *Banksia* subg. *Spathulatae*, spathulate cotyledons also occur in species of */Cryptostomata* and *Dryandra*. Cotyledon shape in *Banksia* and *Dryandra* is also complex and this mapping onto the tree is a misleading oversimplification. Then, above the first

branch they give "Beaked follicles" leading to the remainder of *Banksia* and all *Dryandra*; but not all species of *Dryandra* have beaked follicles (a note in Mast & Givnish, 2002: 1319, citing information received from me, correctly says just that "*Dryandra* commonly has beaked follicles"). That is, the statement in Mast et al. (2005), repeated in Mast and Thiele (2007), that beaked follicle valves are a morphological synapomorphy supporting the holophyly of */Cryptostomata* is not correct, although the character could have been lost secondarily. Finally, in figure 1 (2007), their "Involucre of conspicuous bracts" as a synapomorphy for *Dryandra* is also incorrect. All species of *Banksia* and all species of *Dryandra* have an involucre of bracts subtending the inflorescence. It is correct that in most species of *Banksia* these are inconspicuous (in fact, in many they fall by anthesis), but in several species such as *B. goodii* and *B. victoriae* the involucre is conspicuous and persistent. Conversely, in most species of *Dryandra* the involucre is conspicuous, but in some it is not, e.g., *D. concinna* and *D. sessilis*. Again, the involucre is a complex character suite.

The new *Banksia* subg. *Spathulatae* proposed for the species in clademark */Phanerostomata* is distinguished in the diagnosis thus: "Differing from all other species of *Banksia* in having spathulate cotyledons" (Mast & Thiele, 2007: 65). As just stated, spathulate cotyledons occur in a number of species of *Banksia*, not just those in */Phanerostomata* and they also occur in *Dryandra*—they may be broad or narrow, but they are still spathulate. Hence, Mast and Thiele's diagnosis of their *Banksia* subg. *Spathulatae* is imprecise, though, strictly speaking, there is nothing in the ICN to invalidate it. Their reference under the etymology of the name to "distinctively spathulate cotyledons" without further elaboration indicates an incomplete survey of *Dryandra* and *Banksia*.

Further, the only indication of the taxa that they include in *Banksia* subg. *Spathulatae* (besides the type, *B. integrifolia* L. f.) is a statement in the text on p. 64: "we establish *Banksia* subgen. *Spathulatae* for the species in */Phanerostomata*." There is no reference to where a circumscription of this "clademark" and the taxa included may be found. From mentions of */Phanerostomata* earlier in the paper, one can assume that it is to be found in Mast and Givnish (2002) and/or Mast et al. (2005). The latter includes only nine species of */Phanerostomata* and 20 of */Cryptostomata*, thus not listing some 50 species of *Banksia* s. str. The former lists all species in figures 3, 4, and 6, but figure 6 also includes *Austromuellera trinervia* and *Musgravea heterophylla* in */Phanerostomata*. Presumably the two last taxa are excluded from *Banksia* subg. *Spathulatae* but we are not told this explicitly. From a systematic angle this means that we cannot assign unsampled taxa to these clademarks. Furthermore, the species included in */Phanerostomata* sensu Mast and Givnish (2002) are a very disparate group morphologically. They include some but not all of the "straight-styled" species of section *Banksia* and all the "hook-styled" species of section *Oncostylis*, very distinct sections morphologically and accepted by all since the work of Bentham (1870). In Thiele and Ladiges (1996), they were placed in six series of subgenus *Banksia* (they did not recognize sections). Several infrageneric taxa have been heterogeneous in all generic treatments, but section *Banksia* and section *Oncostylis* remain well defined, so the distribution of their species between */Phanerostomata* and */Cryptostomata* should be investigated further. If the clademark is an evolutionary phenomenon, then there must be character states, however cryptic, that link the included species as a group. More discussion of this would have been informative and, if soundly based, would give more confidence in the reality of *Banksia* subg. *Spathulatae*.

Note, too, that */Phanerostomata* is defined as "typically tall shrubs and trees that occupy moister coastal mountains, especially in eastern Australia, and produce short-lived leaves that are thin, soft and less strongly toothed" (Mast & Givnish, 2002: 1322); but some species included by them do not meet these criteria: e.g., *Banksia nutans*, *B. scabrella*, *B. sphaerocarpa*, *B. grossa*, and *B. incana*, which have tough leaves and occur in Western Australia in open heathlands with relatively low rainfall. Incidentally, in describing the arrangement of the stomata in *Banksia*, Thiele and Ladiges (1996: 669) wrote that "In series *Salicinae*, *Grandes* and *Coccineae*, the pits are relatively indistinct, large, wide and shallow depressions, while in the remaining species they are smaller, more definite, and often crypt-like, with constricted entrances. However, there is a continuous grade between these pit types." This is not the clear distinction implied by Mast and Givnish (2002) in their clademarks. In including *Dryandra* in their concept of */Cryptostomata*, Mast and Thiele (2007) have not said whether they surveyed this character in all taxa of *Dryandra*. Since species of *Dryandra* grow in habitats ranging from forest with relatively high rainfall to inland shrublands with low rainfall, and their leaves range from relatively soft to hard (with or without revolute margins), it is likely that not all belong with the concept of stomatal arrangement in */Cryptostomata*—another area of insufficient research in their work.

A detailed morphological analysis of *Dryandra* (similar to that of Thiele and Ladiges for *Banksia*) is still awaited. For their morphological data on *Dryandra*, Mast and coauthors presumably relied on descriptive work published by previous workers, rather than study the plants to assess whether the molecular data are supported by the morphology. Mast et al. (2005: 86) acknowledged that "we do not have the morphological data that might help to place it [*Dryandra*] when analysed in concert with that sampled in *Banksia* by Thiele and Ladiges (1996)." Further, Mast and Thiele (2007: 65) acknowledged that their results are preliminary, stating that their new classification "is the least disruptive option at present." They referred to "fine-scale taxonomic sampling" being carried out in Mast's laboratory, without explaining what they meant by this. If it is a full morphological analysis of *Dryandra* then this should have been completed before making sweeping nomenclatural changes.

Furthermore...

Mast and Thiele's claim (2007: 64) that an expanded *Banksia* is "a single, easily recognised genus equivalent to the subtribe Banksiinae" is debatable. Separately, *Banksia* and *Dryandra* are readily distinguished morphologically—even people with just basic training have no difficulty recognizing a *Banksia* or a *Dryandra*, even if it is a species that they have not seen before. In fact, combining the two creates a less clearly definable taxon and implies that these authors do not know their plants well. They have not provided an amended description of their *Banksia* s.l., or a comprehensive infrageneric table (see below), or a key to enable people to identify specimens, or even specifically cited works where keys are to be found. Their "automatic" transfer of all taxa recognized by me in *Dryandra* means that they made no reassessment of those taxa. In a complex genus of great morphological diversity, and with new material being added to collections, it is almost certain that a thorough revision would result in changes.

It is noteworthy that Thiele and Ladiges (1996) were unable to determine an outgroup for comparison of *Banksia* and placed subgenus *Isostylis* and subgenus *Banksia* as sister taxa, so that *Isostylis* was basal in their cladograms. The molecular analyses of Mast et al. have consistently placed *Isostylis* as the most advanced group within *Banksia*, as indeed it was in my systematic sequence (George, 1981, 1999a).

Mast et al. (2005: 86) wrote that combining *Dryandra* with *Banksia* "would make *Banksia* the seventh largest genus of vascular plants in Australia." Is this supposed to make us feel good about the merger? They also claimed that it "would probably confer greater research attention on the species of *Dryandra*," and that their inclusion in any comparative study with "exhaustive" taxonomic sampling of *Banksia* "would become certain." These are not scientific arguments, and one can just as easily argue the opposite—that submerging one genus in another (especially at a low infrageneric rank) makes its taxa less conspicuous (Hörandl & Stuessy, 2010: 1647). As stated above, Mast and Thiele should themselves have done far more research before drawing taxonomic conclusions. While this might contribute to our understanding of these fascinating plants, there are many organisms that we hardly know, that are unclassified, to which future direction of such considerable expertise and resources would contribute much more to our knowledge of the world's biodiversity.

Finally, as Winston Churchill might have said, there is some "terminological inexactitude" in the nomenclatural changes of Mast and Thiele. The name *Banksia* ser. *Dryandra* is not just a "comb. nov." but also a "stat. nov." For taxa in *Dryandra* with epithets already occupied in *Banksia*, the designation "nom. nov." is only half the story, as they are also "comb. nov." Also, their use of "basionym" for the replaced names is incorrect—they are not basionyms but replaced synonyms. Several of their new epithets are inappropriate, for example, *obovata* to replace *cuneata* "in reference to the obovate leaf shape" (Mast & Thiele, 2007: 65), when the leaves are typically cuneate, only occasionally obovate; *pellaeifolia* to replace *blechnifolia* "from *Pellaea* a genus of pinnate ferns and *folium* (a leaf), in reference to the divided, fern-like leaves" (no species of *Dryandra* has pinnate leaves).

Infrageneric Classification

Mast and Thiele (2007) have provided minimal data on an infrageneric classification of their expanded *Banksia*. From their figure 1 (cf. Fig. 2 above) we know that they recognize two subgenera, *Banksia* subg. *Banksia* and *Banksia* subg. *Spathulatae*, and one series, *Dryandra*. We can deduce that they recognize the autonym series *Banksia* in subgenus *Banksia*. Beyond that, nothing. They have not said whether they recognize *Banksia* subg. *Isostylis* R. Br. or, if not, which of their subgenera they place it in and at what rank. A phylogenetic tree should reflect the classification of the taxon or taxa concerned, but this is impossible from Mast and Thiele's figure 1, the only figure presented, and which gives only "the major features of the phylogeny."

Their new classification obscures relationships because they have placed all 94 species of *Dryandra* in a single series within *Banksia* while (presumably but not stated explicitly) retaining a comprehensive infrageneric classification for the taxa of *Banksia* s. str. They stated, on p. 64, that the infrageneric classification of *Banksia* "has been tested against phylogenies generated from morphological and molecular data" but did not say which classification they tested or what the results of that testing were. Their subgenus *Spathulatae* contains both straight- and hooked-styled species, but we are left in the dark as to which those species are, and indeed, what infrageneric classification they accept for taxa of *Banksia* s. str. in their expanded genus. Further, with three subgenera and 24 series, *Dryandra* s. str. is at least as diverse as *Banksia*, and this should be reflected in its classification even if it is called *Banksia*. When *Dryandra* is ranked as a series in Mast and Thiele's classification all this information is lost, i.e., their expanded *Banksia* loses predictability.

All we can deduce from their paper about an infrageneric classification is the following:

Banksia
subgenus *Banksia*
series *Banksia* (type, *B. serrata*)
series *Dryandra* (type not stated, presumably *B. formosa*)
subgenus *Spathulatae* (type, *B. integrifolia*)

In other words, while inferences may be made from their background papers, we can place just three of some 172 species in their classificatory scheme with certainty.

Taxonomy in the Face of Uncertainty

Reliance on phylogenetic and cladistic analyses is called into question when one considers the uncertainties and assumptions in many published papers (not to mention the assumptions that lie behind all the computer programs used). As discussed elsewhere in this paper, authors themselves often raise doubts about their results through frequent use of words such as "may/might," "suggest," "appear," and "seem" but make nomenclatural changes regardless. We also have the situation of the same author being involved in the transfer of species from one genus to another (Crisp & Weston, 1987) and then back again a few years later after further research (Chandler et al., 2002), or revising a genus (Crisp, 1995) and then transferring it to another just seven years later (Chandler et al., 2002). The last paper transferred three genera to *Gastrolobium* because their analyses "showed that *Gastrolobium* is paraphyletic" (Chandler et al., 2002: 622) but with no further discussion. Lewis et al. (2005: 4–10), in the section "Changes in generic alignment and tribal composition in the legumes since Polhill (1994)" discussed a number of examples of changes, "reversals," and uncertainties in tribal and generic placement. Crisp and coauthors, and Mast and Thiele, should have done as others faced with inconclusive results have done and undertaken or awaited further research, as was the case for a study of the Chloantheae by Conn et al. (2009: 255) who concluded: "To ensure nomenclatural stability, we recommend that a more comprehensive sample from each of the genera be analysed before formal changes are made." Nonetheless, without further sampling, Conn et al. (2011) presented a new generic classification within the tribe, with associated nomenclatural changes.

A recent paper on *Callitris* and *Actinostrobus* (Piggin & Bruhl, 2010) is a further example of making nomenclatural changes in the face of uncertainty and inadequate assessment of data, in part by the authors being inconsistent in following their own criteria. They (p. 72) regarded bootstrap values of 50%–70% as weakly supported and 70%–90% as moderately supported yet, in their figure 1, six branches had values within the lower range and a further eight were in the moderate range. One branch was below 50% (that leading to Venning's "complex"), and only a single branch (leading to *Actinostrobus*) had strong support (94%). The consistency and retention indexes were also low, at 0.45 and 0.74, respectively. The three species of *Actinostrobus* came out as a robust, holophyletic group in each of their analyses. They listed (p. 74) seven morphological features that distinguish *Actinostrobus* from *Callitris*, although the most distinctive, the presence of sterile scales at the base of female cones, was excluded (without explanation) from their character analysis. Piggin and Bruhl were not confident of their conclusion, stating that "further molecular data are needed to test these results" (2010: abstract, 69). While their data appear to show that *Actinostrobus* makes *Callitris* paraphyletic, they have not shown that the two taxa, when combined, form a holophyletic genus. Yet, with no discussion beyond describing the defence of paraphyletic taxa as "ad hoc," Piggin and Bruhl combined the two genera. Their claim (p. 78) that including *Actinostrobus* within *Callitris* "goes some way towards resolving the instability in [taxonomy of] *Callitris*" appears to mistake where that problem lies—they stated later (p. 80) that "Instability in *Callitris* taxonomy has centred on how to best deal with the seven or eight taxa that make up

Venning's (1979) complex" of *C. glaucophylla* and allies. As all their analyses show, *Actinostrobus* has nothing to do with this group. And, by combining *Actinostrobus* with *Callitris* and not erecting any infrageneric taxon for it, information is lost. The question must be asked: given this uncertainty, why publish these nomenclatural changes? Once again, a refusal to accept paraphyletic taxa has led to an arguably unnecessary combination of genera.

I do not suggest that we await certainty before publishing. If we adopted that approach we would get nowhere. But we should have a firm foundation on which to base major changes in classification and nomenclature, especially those of long standing. Writing about phylogenetic studies, Orthia et al. (2005: 46) wrote, "Studies that do not thoroughly explore the evolutionary history of the study group . . . might be making erroneous or premature judgments about taxonomic boundaries that ultimately perpetuate instability."

Objectivity

Molecular and cladistic analyses are promoted as objective, but many subjective decisions are made in these methodologies (reviewed by Stuessy, 2009a). A critical point is the lack of any objective criterion or measure for determining taxonomic rank in molecular analyses—whether it's flowering plants, bryophytes, reptiles, or fish, the worker makes a subjective assessment of "what looks right." Such analyses are also claimed to be repeatable (and by implication reliable), since the data are available to other researchers at GenBank and analysis of the data can be rerun. But can we readily resample the vouchers for new genetic samples in order to compare analyses (see above for comments on the vouchers used in *Dryandra* and *Banksia*)? Material from other plants of the same species may not give similar results (e.g., Edwards et al., 2010, see above), but unless multiple sampling (both of species and within species) is done, then I contend that the results should be considered preliminary. Although the molecular research program on *Banksia* and *Dryandra* has been running for some 15 years, the results obtained so far are not sufficiently robust to justify major taxonomic changes. The study of morphology is just as repeatable, and we can look at multiple specimens, some the same that previous botanists looked at—such as (in the case of Proteaceae) Robert Brown (1810), Carl Meisner (1856), and George Bentham (1870) in the 19th century, Lawrie Johnson and Barbara Briggs (1975) and others in the 20th.

Mast and Thiele (2007) made a subjective decision on what course to take in resolving their taxonomic problem. Since, according to their cladistic interpretation, they could not maintain the status quo, they considered three options, each of which had varying degrees of support in their analyses, but these levels of support did not enter into their final decision. They discarded their option two (to maintain *Dryandra* and split *Banksia*) because it would require the "establishment of several new, less distinctive genera" (p. 64). This is a subjective decision that we cannot assess because we are not told which species would be placed in which genus and, therefore, cannot consider how distinctive the new genera would be. If they correspond to any of the infrageneric taxa in my classification (George, 1999a), then there are good characters to distinguish them. They discarded option three (to establish two genera equivalent to the clades formed at the basal split of *Banksia*, i.e., */Cryptostomata* and */Phanerostomata*) because it "requires the most complicated nomenclatural changes" (Mast & Thiele, 2007: 64), a reason I have seen no other researcher offer for not proceeding with amending a classification, and again, a subjective decision. Clearly, Mast and Thiele were prepared to consider recognizing multiple genera on less than 100% support, but, in effect, they took the easy way out by adopting their option one, to reduce *Dryandra* to a synonym of *Banksia*.

The Concept of the Genus

The question of generic delimitation and size has occupied a number of authors. For example, Pfeil and Crisp (2005), in a section entitled "Is a genus real, and if so, in what sense?," stated that their concept of genera is "groups of organisms more inclusive than a single species." In a paper in the same number of *Australian Systematic Botany*, however, Orthia et al. (2005) appear to accept monotypic genera such as *Euchilopsis*, stating (p. 43) that "there is nothing wrong in principle with the circumscription of small or monotypic genera" but later (p. 46) indicate that they would have a problem with many small genera that had "the same status" as large genera. They felt that splitting *Pultenaea* s.l. into multiple genera, as their cladistic analysis indicates, "would introduce greater taxonomic inequivalence, maintain instability and enforce monophyly onto reticulate groups within it" (p. 46). As mentioned above, Edwards et al. (2010) also had problems with small genera. As Hörandl (2010: 349) has pointed out, however, "If rapid morphological divergence occurs in single

lineages, then a classification of monotypic genera is more informative about this divergence than classifying a heterogeneous clade as a taxon." There is nothing scientifically wrong with the concept of small genera. Almost certainly, every genus in its beginning was monotypic.

As mentioned above, Humphreys and Linder (2009), in their work on danthonioid grasses, decided not to adhere to the concept of larger monophyletic (holophyletic) genera over several small ones since it would have practical disadvantages. They wrote (p. 1054):

> "Stability" increases communication power of a classification by perpetuated use of already accepted names . . . and is maintained by delimitation of genera in such a way that future nomenclatural changes will be unnecessary. . . . efforts to define a genus that reflects evolutionary patterns should not override those that ensure its usefulness. Consequently, monophyly is important only in so far as it increases the chances of a genus being both stable and predictive.

As Nyffeler and Eggli have written (2010: 237), "Discordance between molecular phylogenies and traditional classification practice should rather be seen as a challenge to further investigate morphological characteristics potentially useful for circumscribing and identifying taxa derived from inferred phylogenetic relationships." Mast and Thiele's work did not take up this challenge. It is to be hoped that Edwards et al. do so before making nomenclatural changes in Melaleuceae.

There has even been a move away from considering morphology useful in phylogenetic and taxonomic analyses, e.g., a paper by Scotland et al. (2003). The ultimate view is that of Tautz et al. (2003) who argued for taxonomy based solely on DNA, discussed with counter arguments by Lipscomb et al. (2003). A similar divergence of views in zoology was discussed by Mooi and Gill (2010). Morphology still has an important role in biological classification, but who knows where future theory will lead?

The Role of Australian Herbaria in Evaluating Nomenclatural Changes for the Australian Plant Census

The Australian Plant Census (APC) is a database of the accepted scientific names for the Australian vascular flora, both native and introduced, and lists synonyms and misapplications for these names (see <http://www.chah.gov.au/apc/about-APC.html>). The APC will cover all published scientific plant names used in an Australian context in the taxonomic literature, but excludes taxa (including cultivars) known only from cultivation in Australia. The APC "represents the considered opinion and nomenclatural research of [a convenor], 16 members of the APC Working Group, researchers that the Working Group consult in each herbarium, 8 Heads of Herbaria, 4 APC data entry people and user groups such as ABRS [Australian Biological Resources Study]" (Orchard, 2006: 30).

Discussing alternative taxonomies in relation to Australia's Virtual Herbarium (AVH), Entwisle and Weston (2005: 1) wrote that "for day-to-day business and pleasure, we [Australian taxonomists] must deliver 'what the customer wants.'" The same guidelines were to be used for the APC:

Guideline 1: Where possible, named taxa should be monophyletic based on current reliable evidence. This is qualified by Entwisle and Weston (2005: 2): ". . . there are times when we need to accept higher taxa [above species] that are not monophyletic, at least in the short term [earlier defined as 'e.g. 10 years'] . . . [such as] when different lines of evidence (especially molecular *v.* morphological) are in conflict." I believe that "monophyletic" is used here in its narrow sense, i.e., = holophyletic. As discussed above, paraphyletic taxa should be accepted, especially where supported by the morphology. In this case we have a monophyletic taxon (*Dryandra*) and a paraphyletic but easily defined one (*Banksia* sensu George, 1981, 1999a). Regardless of this, I suggest that this is a case where there is conflict between molecular and morphological evidence, and that acceptance of the transfer within a few months of publication was too rapid.

Guideline 2: Minimize taxonomic change (across Australia as a primary focus). In their discussion, Entwisle and Weston (2005: 2) say that "accepting stability . . . should result in both information gain and minimisation of nomenclatural confusion." The transfer of *Dryandra*, with 95 species and 41 infraspecific taxa arranged in a recently published infrageneric classification (George, 1996; Cavanagh & Pieroni, 2006), to *Banksia* and there placed in a single series, has done just the opposite—established some 135 new combinations and lost all the subdivision within *Dryandra*.

Guideline 3: Change is more acceptable in groups that are not "charismatic," not economically important, or do not have a substantial "interest group." Dryandras occur naturally only in Western Australia, where they are both charismatic and economically important. Further, there are significant "interest groups" for *Dryandra* and *Banksia* (Australian Native Plants Society Study Groups).

Guideline 4: The preferred "name" should be as scientifically defensible as possible, but its acceptance does not imply that it is necessarily the "best name" on scientific and/or social grounds. The scientific part of this guideline seems self-contradictory: perhaps it should be "as scientifically defensible as possible" yet not necessarily the "best name on scientific . . . grounds." I argue that *Banksia* s.l., as the current preferred name for the APC, is neither well justified scientifically nor the better name on social grounds.

Guideline 5: Avoid epithets already in use in possible congeners. This is not relevant to the current matter.

Guideline 6: The preferred name is that used in most states and territories ("majority rules"). The decision should still be based on good science. In 2004, the Council of Heads of Australian Herbaria established a committee to "make judgements on any contentious conflicts" (Entwisle & Weston, 2005: 4). This is discussed further below.

Mast and Thiele (2007) referred to these guidelines but cited only numbers 1 and 2. They agreed with the criteria but ignored Entwisle and Weston's qualifiers (2005). They wrote: "monophyly is sensible at ranks higher than species, given that this restriction makes taxa more predictive of character-state distributions, and provides a clearer reflection of phylogenetic relationships than when non-monophyletic taxa are permitted" (p. 64). Why does monophyly (holophyly) make taxa "more predictive of character-state distributions" and provide "a clearer reflection of phylogenetic relationships than when non-monophyletic taxa are permitted" (p. 64)? It's easy to say that X is (closely) related to Y, and a lot easier to discuss genera X and Y than genus X subgenus X and genus X subgenus Y. Also, the larger a genus, the larger and more complex the range of characters and states, hence the more difficult it may be to be predictive and see relationships within it. Biological names are about communication.

In the preface (pp. i, ii) to the special issue of *Australian Systematic Botany* (Barrett et al., 2005) in which these guidelines and the article by Mast et al. (2005) were published, the editors (Barrett, Hopper, and Farrer, though attributed to only Barrett in the Contents) commented several times on the need for caution before accepting some generic changes. They wrote: "we can best serve the end-users of our classifications by maintaining '*status quo*' until we are confident that our data are sufficient to provide a stable classification" (p. i); and later "In the case of *Banksia/Dryandra*, it is easy to recognize two 'genera' on morphological grounds and many will prefer to do so, even though this renders *Banksia* paraphyletic. The classification as two genera is considered by some to be more practical, even if it does not reflect true genetic relationships in the group concerned" (p. i). As stated above, even Mast and Thiele (2007) considered their results to be preliminary, stating that their new classification "is the least disruptive option *at present* [my italics] (p. 64)."

Discussing changes in the nomenclature of orchids, Barker and Bates (2008: 101) wrote that "Herbaria, among other institutions, tend to adopt a conservative approach in the adoption of new names, preferring to wait until there has been sufficient testing of new concepts and hence greater stability and acceptance of these names . . . Rushing in and adopting name changes as they occur can lead to a later reversal of a decision and an unnecessary confusion of names." Strict adherence to holophyletic taxa is also counterproductive for the users of plant names—see, for example, Brickell et al. (2008). When well-known, morphologically distinguishable, and identifiable genera are merged, it causes confusion, hinders communication, and can lead to loss or obscuring of information for those users. Examples (summarized by Brickell et al., 2008) include placing the Cactaceae in Portulacaceae, *Rafflesia* in Euphorbiaceae, and placing six well-known genera in *Primula*.

Farjon (2007: 641) wrote: "Taxonomy should be a science that earns its respect from users as well as fellow scientists. If it insists on strict adherence to a spurious dictum, more appropriate to a religious sect than to science, it will lose that respect."

Grant (2003: 1268) also wrote about the roles of taxonomic and cladistic products in society:

> There is a long-standing social need for similarity/difference classifications. This is why they have existed since prehistoric times. . . . In modern societies, taxonomic classifications are used for identification and information retrieval by the general public, by people in technological fields, and in biological research (including cladistics).
>
> Cladistics has no such general constituency. Phylogeny is of only secondary interest to most people including most kinds of biologists. Who needs a crocodile-bird clade when we already have a bird taxon and a crocodile taxon?

All these guidelines and considerations advise caution when deciding whether to adopt taxonomic and nomenclatural changes for the APC, especially of large groups. Yet the APC committee has ignored them in the case of *Banksia* and *Dryandra*. As far as I am aware, there has been no published report on how the Group reached its decision to accept *Banksia* s.l. or whether there was any discussion. Members agreed in response to a request by e-mail (B. Lepschi, CANB, in correspondence). A letter on the subject to the editor of

the Friends of the Australian National Botanic Gardens Newsletter no. 61 (<http://friendsanbg.org.au/newweb_drupal/sites/default/files/pdf/newsmar09.pdf>), reprinted in the *Dryandra* Study Group Newsletter no. 57, states just that the "Australian Plant Census ... represents the consensus view of Australian state and territory herbaria, as ratified by the Council of Heads of Australasian Herbaria" (Lepschi et al., 2009).

The website for the APC (<http://www.anbg.gov.au/cgi-bin/apclist>; accessed 22 April 2010) tells us only that *Dryandra* is a "synonym of Banksia L. f. nom. cons." However, many people with a working knowledge of these plants have rejected the merger. For example, the Banksia and Dryandra Study Groups have considered the merger and rejected it. The Wildflower Society of Western Australia continues to use *Dryandra*. Notably, the Botanic Gardens of Adelaide listed *Dryandra* in their 2010 catalogue of plants being grown there, despite the Gardens' own herbarium accepting the merger three years earlier. Also, in a paper coauthored by Mast (Sauquet et al., 2009), *Banksia* and *Dryandra* were considered as genera except for their final analysis: "For practical reasons [not explained], we do not follow this nomenclatural change [the merger of the two genera] here but we have included several species of *Banksia* as terminal taxa in our dataset and only consider Banksiinae (the monophyletic group of all species of *Banksia* and *Dryandra*) as a terminal taxon in all diversification rate analyses." In the paper, tables S5 (species numbers) and S6 (voucher information and GenBank accessions) list *Banksia* and *Dryandra* separately. He et al. (2011) retained *Banksia* s. str. Thus, we are left with the situation of Australian herbaria using one nomenclature and the "customers" another.

Conclusion

The molecular analysis of *Dryandra*, though limited in scope, has supported its close relationship to *Banksia*, but the decision to merge two genera that are iconic in the flora of southwestern Australia is based upon insufficient research and a concept that genera cannot be paraphyletic. Phylogenetic analysis can provide a useful hypothesis, but the results should be used cautiously, and not used to make premature changes in classification that may later be overturned. As Hörandl and Stuessy (2010: 1650, 1651) wrote, "Paraphyletic groups routinely originate as part of the evolutionary process, and they, therefore, have an important role to play in classification. ... Paraphyletic and holophyletic status should be used as features of taxa, describing their evolutionary status, not as criteria for their acceptance in classification." In a way it seems that, with strict cladistics, we have come full circle from the artificial system of taxonomy of Linnaeus to the artificial system of cladistics. Significantly, while the research discussed here may make *Banksia* paraphyletic with respect to *Dryandra*, it has not demonstrated conclusively that *Banksia* and *Dryandra* together are holophyletic. Those who know *Dryandra* and *Banksia* well accept the close relationship and have no difficulty distinguishing them on morphological grounds. Under the International Code of Nomenclature for algae, fungi, and plants (McNeill et al., 2012) there is no requirement to accept this merger, and many users of plant names have continued to use *Dryandra* and *Banksia*. Australian herbaria should follow their own guidelines and do likewise.

Two apomorphic states are clear cut in distinguishing *Dryandra* from *Banksia* s. str.—the receptacle is flat or only slightly convex or concave, and the common and floral bracts are openly arranged. In *Banksia* the receptacle is ovoid to cylindrical, and the common and floral bracts are tightly packed.

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